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THE RELATIONSHIPS OF ANOLIS OF THE ROQUET SPECIES GROUP (SAURIA:IGUANIDAE) — III. COMPARATIVE STUDY OF DISPLAY BEHAVIOR

George C. Gorman¹

INTRODUCTION

In separate papers on chromosome cytology and electrophoresis of blood proteins (Gorman and Dessauer, 1966; Gorman and Atkins, 1967), the relationships of the *roquet* group of *Anolis* have been discussed in detail. The present paper is an attempt to use comparative ethology as an additional index of relationship and evolutionary history of the group. No attempt is made here to provide an "ethogram" of any of the forms. Instead, some stereotyped action patterns that vary from island population to island population are compared as taxonomic characters.

Taxonomy and Distribution

Eight forms are considered in this paper. The species of the *roquet* group are found on all the islands of the Lesser Antilles from Martinique south to Grenada and west to Bonaire. To the north of Martinique are anoles of the *bimaculatus* group; to the south, on Trinidad (a continental island), and to the west, on Curacao and Aruba, are members of the *chrysolepis* group (classification into species groups follows Etheridge, 1960). These species groups seem to exclude each other, and the only recorded overlaps (on Trinidad, St. Lucia, and Guayana) appear to be recent introductions (Gorman and Dessauer, 1965, 1966). Figure 1 summarizes the distribution of the group.

¹ Present address: Museum of Vertebrate Zoology, University of California, Berkeley, California.

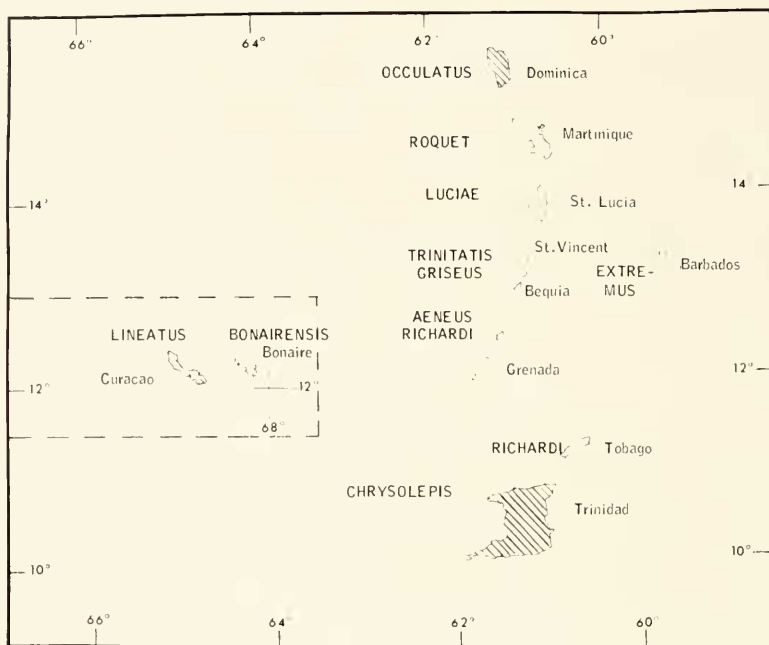


Figure 1. The distribution of *Anolis* of the *roquet* species group (un-hatched islands). Names of forms considered, in capitals. Names of islands, in capital and small letters. The anoles on the islands indicated by oblique lines are not in the *roquet* group.

By the use of chromosomes and blood proteins, the species group has been divided into several subgroups and species designated. A basic dichotomy exists in chromosome number. Three forms have $2n=34$, the other five have $2n=36$. The latter is the presumably primitive number for the family Iguanidae (Gorman, Atkins, and Holzinger, 1967).

Those anoles with reduced diploid number have always been considered very closely related on morphological evidence. Reduction in chromosome number is rare and generally an advanced character, and this is taken as additional evidence that indeed these three anoles form a natural subgrouping. For reasons documented elsewhere (Gorman and Dessauer, 1966), similarity in

hemoglobins was used to define species. Thus the group could be divided in the following manner:

$$2n = 36 \left\{ \begin{array}{l} \textit{luciae} \\ \textit{trinitatis} \\ \textit{bonairensis} \\ \textit{richardi richardi} \\ \textit{richardi griseus} \end{array} \right. \quad 2n = 34 \left\{ \begin{array}{l} \textit{roquet roquet} \\ \textit{roquet extremus} \\ \textit{aeneus} \end{array} \right\} \begin{array}{l} \text{common Hb} \\ \text{common Hb} \end{array}$$

In the $2n=36$ group (primitive) *A. r. richardi* and *A. r. griseus* form a natural subunit characterized not only by proteins but by giant size.

An hypothesis about the biogeographic movements of the group is being presented in a separate paper (Gorman and Atkins, 1968). The defense of this hypothesis will not be repeated here. However, it is presented as a working model with which the behavioral results may be compared.

A. luciae is considered the most primitive member of the group. Reasons include chromosome number, size (intermediate between the giants and the other five forms), and geographic position (more or less in the center of the group.) From St. Lucia, St. Vincent was twice colonized, leading to two species, *trinitatis* (small) and *griseus* (giant). From St. Vincent, the two reached Grenada and through further differentiation have become *aeneus* (small) and *richardi* (giant). *A. richardi* has reached Tobago without further differentiation. The small Grenada species colonized Barbados (*extremus*) and from there Martinique (*roquet*). Or, alternatively, the small St. Vincent form (*trinitatis*) colonized Barbados directly, followed by a double radiation from Barbados to Grenada and Martinique.

Behavior in *Anolis*

Because of the elaborate displays of these strongly territorial lizards, the *Anolis* species have been of long-standing ethological interest. Greenberg and Noble (1944) presented the most comprehensive discussion of a single species, *A. carolinensis*. This report was based upon four years of observation of approximately 600 lizards. Included in their paper are sections on aggression, courtship and mating, egg laying, dominance, subordination and hierarchies, territory, and sex recognition. Other studies, such as Kästle's (1963) on *Norops* (= *Anolis*) *auratus*, Carpenter's (1965) on *A. townsendi*, and Evans' (1938) on *A. sagrei*, provide valuable descriptions of displays and social behavior in single species.

The only attempt at a broad comparative survey of *Anolis* behavior was by Ruibal (1967), who described aggressive displays in twelve species of Greater Antillean *Anolis*.

The genus is divided into two major groups (alpha and beta), based on an osteological difference (Etheridge, 1960), and supported independently by chromosome differences (Gorman, 1965). Ruibal (1967) was interested in determining if there was any parallel between the alpha-beta dichotomy and behavior. Although Ruibal found species-specific differences, he wrote, "the analysis of the initial response in these anoles demonstrates that the behavioral patterns are of limited value in determining relationships within the West Indian species of *Anolis*."

My own study, presented here, indicates the value of behavior as a systematic character *within* at least one species group.

METHODS

In 1963-64, I spent 10 months in the Caribbean area, based at the University of the West Indies in Trinidad. Subsequently, several additional brief visits were made to the islands where the *roquet* group occurs, as well as to neighboring islands. At first, the lizards were simply observed in the field and extensive notes on ecology and behavior were prepared. Later, they were studied in cages at the University of the West Indies. In general, two adult males were placed on opposite sides of an opaque partitioned cage. Several hours to days later, the partition would be removed and social interactions described. To gather quantifiable data the lizards were photographed on 16 mm motion picture film. The bulk of the data presented are from analysis of films made in the field. In some cases the films are of natural interaction, but high intensity territorial disputes are not frequent in natural situations; they are easily elicited, however, by tethering an "intruder" to a long pole and placing him within the territory of a resident. Films were analyzed on a Weinberg-Watson single frame analyst. This allows frame-by-frame analysis of the temporal sequence of displays. Amplitudes of movements were not measured precisely but were estimated. No great emphasis has been placed upon amplitude differences in display.

ELICITATION OF DISPLAY

Iguanids respond to visual cues. The introduction of a mirror into a cage elicited highly stereotyped displays identical to those

seen in the field in natural encounters. Carpenter (1962) has reported results of mirror experiments in *Sceloporus*, and a rather accurate description of an *A. roquet extremus* display to a mirror was written for a popular audience by Dr. Maurice Burton (London Illustrated News, 29 August 1964).

Neither the opponent's dewlap color nor the dewlap *per se* seems to be of great importance in eliciting a response from a resident. Greenberg and Noble (1944) found that restraining the dewlap by means of a collodian coating did not affect the social status of the male. Dominant animals were still able to hold territory and win combats with normal rivals. In addition, normal males displayed to males unable to extend the dewlap.

I have found that members of the *roquet* group in captivity will display to other species if these are in the same size range.

A planned experiment to study releasers by use of models presented to residents in the field was thwarted at the outset. *A. trinitatis* are very abundant and quite willing to display to other anoles in the Botanic Garden in St. Vincent. A life-size wooden model of a male *trinitatis* was constructed and, I thought, accurately painted. A slit was made in the throat region for insertion of paper dewlaps of the "right" or "wrong" color. If males responded aggressively to the model, then variations in size and color were planned to elucidate exactly which parameters were important to a resident territorial male. However, responses to the dummy were uniformly negative.

Experiments involving a decapitated intruder were somewhat more successful. The decapitated head was pinned to a piece of sponge, cut approximately in the shape of a lizard torso. Several resident males attacked and/or displayed actively to this model, and even to the decapitated head alone, when dangled freely. This experiment was terminated when a *griseus* ran down from the crown of a tree and grabbed and ate the *trinitatis* head.

In a reciprocal trial, a head-sized piece of sponge was pinned to the body of the decapitated lizard. This did not elicit aggressive display. Some males were painted bright red, others bright white. Results in several trials were equivocal. Some residents displayed or attacked, others fled from the intruder. Thus, something in the configuration of the head probably acts as a releaser.

Another apparently important component in elicitation of display is movement on the part of the intruder. A tethered male will usually flatten himself on the substratum in a classically submissive

posture.¹ The resident will watch. Slight jiggling of the intruder is sufficient to elicit immediately a high intensity response (biting attack or display).

DESCRIPTION OF DISPLAY

Carpenter (1962) has standardized his descriptions of iguanid behavior by describing eight characteristics of display — site, position, posture, movement type, parts moved, units of movement, sequence, and cadence.

Ruibal listed and defined the following movements and postures to describe aggressive encounters in *Anolis*.

1. Dewlapping — the characteristic erection of the large gular appendage.
2. Bobbing — the vertical motion of the head.
3. Pushups — an extension of the limbs to raise the body off the ground.
4. Tail wags — vertical or horizontal movement of the tail.
5. Tail lashes — a very exaggerated movement of the tail in a broad whipping manner.
6. Tongue — the tongue may be everted and protruded from the mouth and in some species may become purple with engorged blood.
7. Nuchal and dorsal crests — the dorsal regional of the neck and the middorsal region of the body are usually raised as thin fins.

Application of these descriptions to the *roquet* species group would be as follows:

A. The eight categories of Carpenter.

1. Site: All the anoles of the *roquet* group are strongly arboreal. Most daytime observations are made of animals on tree trunks four to seven feet above the ground. Most displays are given when the lizards are on tree trunks; however, during a battle they will display from the ground. When they display they try to find a slightly elevated site, such as a knot on a tree.

2. Position: Orientation is usually perpendicular to the recipient of the display. If the opponents are parallel, then the heads are facing each other. The position chosen maximizes the opponent's view.

¹ Darwin (1872) pointed out that submissive postures were often the antitheses of aggressive ones. Thus, in the anoles in submissive posture the crests are down, dewlap in, body low.

3. Posture: In aggressive encounters, nuchal and dorsal crests are generally raised. As noted by Greenberg and Noble (1944) for *A. carolinensis*, "The initial hostile reaction is a puffing or gorging of the throat followed almost immediately by lateral flattening so that the male appears much larger from side view." This serves as an excellent description for the *roquet* group and shall be referred to as "engorged head."

These three categories are not of further use in this comparative study because they are constant for the species group.

4-6. Movement type, parts moved, and units of movement are encompassed by Ruibal's categories, and are discussed below.

7. Sequence: The order of appearance of units of movement will be exemplified by quotations from notes on actual encounters.

These categories again are consistent for the species group.

8. The measured time for the performance of each unit of movement. This is the important category employed in comparing displays within the species group.

B. The seven movements of Ruibal.

1. Dewlapping: The dewlap of the *roquet* group and all its near neighbors is well developed. The cadence of extension differs between the *roquet* group and the anoles that geographically surround it.

2. Bobbing: In the *roquet* group all eight forms bob the head in high intensity display, and each form shows a temporal sequence that is unique. I also refer to nodding, in which the head is raised and lowered very slowly. This is a less stereotyped movement and seems to occur at lower intensity.

3. Pushups: Again, all forms in the group rise up on all limbs in high intensity display. Some have also been observed to include "rhythmic movements" as a part of the challenge display. This is a series of movements at very precise intervals — it may simply be head bobs, or pushups, or pulsating locomotion.

4. Tail wags: Horizontal movement of the tail is seen under situations of stress. It occurs when two anoles are actually fighting and is not seen in the clearly dominant animal. It also occurs when an anole is captured by a herpetologist and is held in the hand.

5. Tail lashes: All species of the *roquet* group may use the tail in a challenge display. The frequency and amplitude of tail lashes is an important character in tracing relationships.

6. Tongue: Several members of the *roquet group* have been seen to protrude the tongue during display. I do not know how frequent or how widespread this movement is. The tongue is

engorged with blood and quite bright in color. At the termination of the display, while the dewlap is being retracted, the mouth is opened and closed several times as though a swallowing movement were occurring. This has been recorded for *A. r. roquet*, *A. trinitatis* and *A. bonairensis* and may be present in the other species.

7. Nuchal and dorsal crests: Present and raised in all species during aggressive encounters.

THE DISPLAY CATEGORIES OF THE ROQUET GROUP OF ANOLIS

There are three obvious categories of display in this species group: activity bobs, courtship, and aggressive display. Only the last was studied in detail.

(1) The activity bob corresponds to Carpenter's (1962) "Assertion Display." For example, in changing position a lizard may run a few feet, stop, bob, run a few more feet, stop, bob, etc. This bob is also commonly seen after feeding. I have reason to believe that it is stereotyped and may be species-specific. However, I do not have enough data to discuss it further. This bob is most commonly given by females.

(2) Courtship was difficult to study under field conditions, as most displays directed by males to females were followed by rapid departure by the female. There are no obvious differences among the species in courtship display, and my observations are concordant with those of Greenberg and Noble (1944) on the following points:

a) There is no sign of aggression; *i.e.*, engorged head, crest erection, and tail jerks are all absent.

b) The approach pattern differs from the aggressive encounter in that there are numerous rapid low amplitude bobs and an irregular, jerking walk.

(3) Aggressive display.

The most elaborate of the displays are also the most stereotyped, hence the most useful for analysis of evolutionary relationships. Intensity of display obviously varies, as has been pointed out by Kästle (1963) and Ruibal (1967). Ruibal limited his study to what he called the "initial response," which he defined as "the immediate and first response of the test animal to the decoy." Later he states that it is comparable but not identical to the challenge display of Carpenter (1962) — "the initial response actually represents the first part of the challenge display."

I agree completely with Ruibal that there is a predictable, stereotyped portion of lizard display behavior. However, the term "initial" in Ruibal's phraseology is unfortunate, because the literally immediate response of a resident male to an intruder is quite unpredictable: the resident may flee, go into the engorged head posture and wait, attack by biting, or display at varying intensities. I prefer to use the term challenge display.

All eight members of the *roquet* group have challenge displays which follow a definite sequence of actions: (1) extend dewlap; (2) rise high on all four limbs; (3) raise the tail, then lower it; (4) lower the body; (5) give rapid head bob; (6) retract dewlap.

The following excerpt from my field notes will exemplify this pattern:

A. r. roquet — Martinique — 2 July 1965:

A tethered male intruder is placed about 12 inches above a resident male (R) perched on a tree. The intruder starts running away from resident. R slowly moves up several inches, pauses. Intruder jiggled. R backs away. R turns perpendicular to intruder. Intruder moves and R follows, stopping a foot above. Head is in engorged position. R moves to two feet above intruder; extends dewlap fully; rises high on all four limbs; 5 tail lashes; lowers body; dewlap half retracted. R pauses for several seconds. Extends dewlap fully while body rising high on all four limbs. Tail raised high and then lowered slowly. Bobs head. Retracts dewlap. Display is repeated again.

Note that the sequence of movements is the same in the two full displays, but in the first instance head bobbing did not follow the tail movement.

The six sequential steps of the challenge display are present or absent in independent fashion, but when they do appear they are evidently never out of order. That is, the dewlap might not be extended but the resident male still lashes his tail and then bobs; or he may omit the bobs, or he may not fully retract the dewlap at the end of the sequence. However, he will never bob, then lash the tail, and then extend the dewlap.

Some of the steps are better correlated than others. The tail movement almost always occurs with the dewlap fully extended. And, if there be a rapid bob with dewlap extended, the dewlap is almost always retracted at the end of the sequence unless the displaying lizard immediately launches into a new sequence.

The high intensity challenge display is interpreted as occurring when there is an intermingling of attack and withdrawal stimuli. The elaborate display is often preceded by backing away from the intruder. Indeed, the displays often follow unsuccessful direct

attacks. The following encounters may serve as illustrations.

1. *A. trinitatis* — St. Vincent — 8 July 1966:

Intruder is placed three feet below resident who is 10 feet up in a coconut tree. R runs down, bites at intruder. Bites again. They lock jaws. R breaks away and runs back up. Bobs rapidly. Attacks again several times, biting at the head of intruder. R backs away. Extends dewlap half-way. Rapid bob. R attacks again. Grab jaws. R flipped to ground.

2. *A. r. roquet* — Martinique — 3 July 1965:

Tethered male intruder placed four feet below resident who turns immediately, runs down and stops one foot above intruder. Pauses. Then rushes at intruder and bites at head; extends dewlap, hobs. Runs jerkily above intruder; full dewlap extension, head bob, dewlap slowly retracted. This is repeated again. Then R moves toward intruder and bites at him. R then backs away and moves to one foot above intruder. Dewlap fully extended, head bobs, then dewlap retracted. Repeated several times. Each time there is a slight movement of the intruder, there has been a full dewlap extension followed by head bobbing. Resident then runs to one foot above intruder. Faces down and is approximately perpendicular. Rises high on all four limbs, tail comes up slowly; full dewlap extension; body lowered, head bob, dewlap retracted. Then R moves up and away from intruder.

In Trinidad, I filmed a long sequence of a male *A. aeneus* displaying to a tethered intruder in which the resident gave the full display, then ran up and away from the intruder. I then moved the intruder up a comparable distance, the resident again quickly displayed and moved away again. This was repeated several more times.

These examples serve to support the hypothesis that the elaborate challenge display is not simply a ritualization to avoid physical fighting, but rather a display given in a situation with conflicting stimuli of attack and flee. Under natural field conditions these displays have been seen only when the opponents were extremely evenly matched. Usually the engorged head of a dominant resident is enough to stimulate flight in a subordinate or intruding male.

Combat is by no means always the initial high intensity response, as the following notes indicate.

A. r. roquet — Martinique — 3 July 1965:

Intruder placed near male resident who immediately goes into engorged head posture and moves down toward intruder. R extends dewlap fully and rises up on all four limbs; three tail lashes; dewlap slowly retracted.

Some encounters are settled without actual biting. I once witnessed a very lengthy dispute between two male *A. trinitatis* in

the Botanic Gardens of St. Vincent. Both were on a broad tree. At the start, one was about two feet above the other. After some fifteen minutes with dozens of high intensity displays, they slowly moved towards one another and, when contact was made, they butted heads, snouts pointing downwards. Then one backed off and climbed up and around the tree.

Although all these encounters describe males, females also display to females. Although the secondary sexual characters of dewlap and crests are much reduced, and the females are also much smaller than adult males, the postures and motions appear identical to those of males. I never saw a natural interaction between females, but did observe and film female display by use of a tethered intruder.

SYSTEMATIC SECTION

I. DEFINITION OF THE *roquet* SPECIES GROUP ON THE BASIS OF BEHAVIOR

Although each of the eight forms has a display which is quite distinct because of variation in cadence, all members of the species group have basically a very similar display. In the use of the dewlap, the *roquet* group differs from its near neighbors in the *chrysolepis* and *bimaculatus* groups. Thus, behavior provides further evidence that the group is a natural evolutionary unit.

In all eight forms, the dewlap is extended and held out for the entire display sequence, and sometimes is not retracted at the end of the sequence. The dewlap is never pumped in and out in any rhythmic manner. This contrasts sharply with the other Lesser Antillean anoles. Figure 2 illustrates the challenge display of *A. roquet extremus*.

In place of the activity bob, members of the *bimaculatus* group seem to have a true assertion display *sensu* Carpenter. I have watched and filmed *A. oculatus* on Dominica pumping the dewlap in and out in a slow rhythmic manner — even when no recipient of the display was apparently present. In high intensity challenge, dewlap pumping is an integral part of a complex display which also involves bobbing and tail movements.

A. lineatus (*chrysolepis* series of beta anoles) of Curacao also pumps the dewlap. This species is quite unrelated to the *bimaculatus* group (alpha anoles), and serves to illustrate the problem Ruibal (1967) encountered in a search for a major diagnostic character to split the genus by means of behavior.



Figure 2. Challenge display of *A. roquet extremus*. Dewlap fully extended, tail up, and body high off the perch.

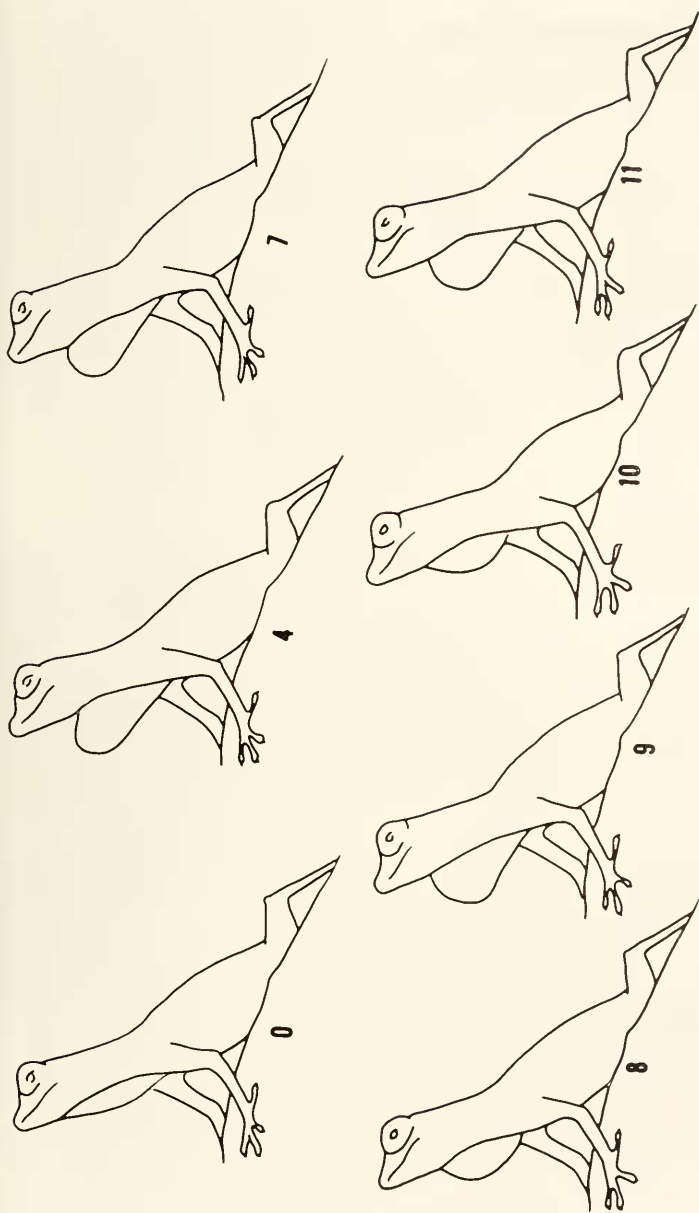


Figure 3. The challenge display of *A. chrysoplepis*. This consists of rapid flashes of the dewlap while the body is in a stationary position. The drawings are from a display filmed at 16 frames per second. The number under each drawing corresponds to the number of frames (time elapsed in units of sixteenths of a second from starting time 0).

A. chrysolepis of Trinidad and the South American mainland displays by flashing the dewlap extremely rapidly and in a stereotyped manner. The entire display appears to consist of dewlapping. The head is held high but is not bobbed. Figure 3 shows *chrysolepis* in challenge positions.

Because dewlapping is widespread in both the alpha and beta anoles, it is interpreted as a primitive character which has been secondarily lost in the *roquet* group. Further evidence for this will be presented below.

II. DESCRIPTION OF THE CHALLENGE DISPLAY OF *A. luciae*

A. luciae is considered the most primitive member of the species group. It is thus worth analyzing its display in some detail, to serve as a basis for comparison.

Descriptions of interactions

1. Forestiere, St. Lucia — 6 July 1965

Resident male is high in a tree. Tethered intruder placed four feet below him. R rises up on all limbs, extends dewlap, tail goes up once, then down. Bobs head. There are four distinct series of bobs while the dewlap is held out. Dewlap slowly retracted.

2. Vigie Beach, St. Lucia — 6 July 1965

Resident male is in a breadfruit tree. Intruder placed one foot below him. R immediately orients perpendicularly to intruder, head facing head. Resident rises up high. Extends dewlap and bobs head. The head bobs are in four distinct series, with a partial dewlap retraction following each series. Intruder turns, and R turns, maintaining perpendicular orientation. Repeats display, again with four series on a single dewlap.

The display of *luciae* may be characterized as distinct from other members of the *roquet* group by the following:

1) Tail — the tail is infrequently used in display sequence. When it is used, it is raised once slowly, then lowered.

2) Head bobs — *luciae* has a head bob sequence that is extremely long in duration and that is clearly divided into several series. That is, a series of bobs is followed by a pause, followed by a series of bobs, followed by a pause, etc. (Figs. 4L and 5L).

3) Partial dewlap retraction — during the long pauses, the dewlap is very slightly retracted, then re-extended. *A. luciae* is the only member of this species group to move the dewlap at all

in mid-sequence. This movement might be a vestige of the dewlap pumping common to most *Anolis*.

The following quantitative data were analyzed:

1) Number of peaks preceding a pause. A pause was arbitrarily defined as 6/16 of a second (N.B. all films were made at 16 frames/second, and time units discussed are in 16th of a second or frame) with no head movement. A peak was defined as the highest point the head reached before the next downward movement. Thus sub-peaks were not counted. The distribution in number of peaks per bobbing series proved to be quite variable, with a range from 1-18. However, the mean is 5.2 and 54 per cent of the sequences had 4, 5 or 6 peaks.

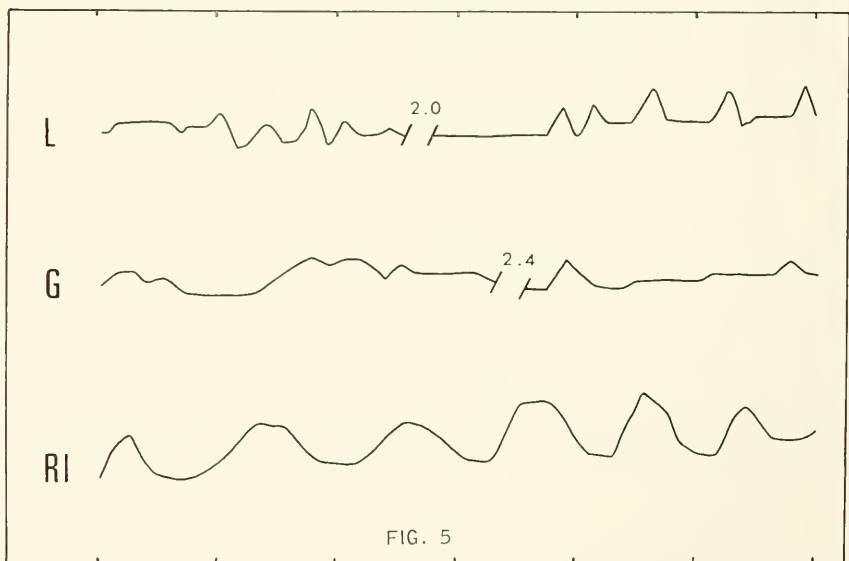
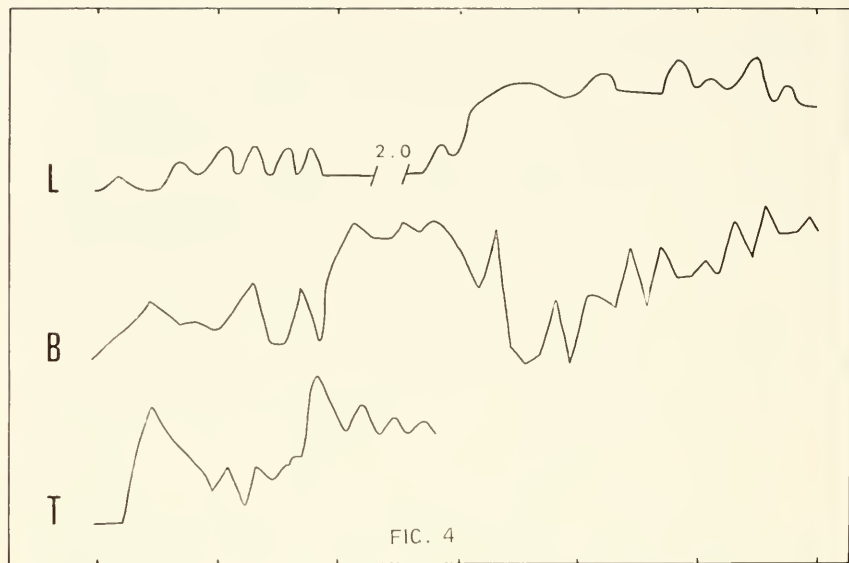
2) The time interval of bobbing series was also measured. Again the range is very broad, 2-47 frames. The mean is 18.

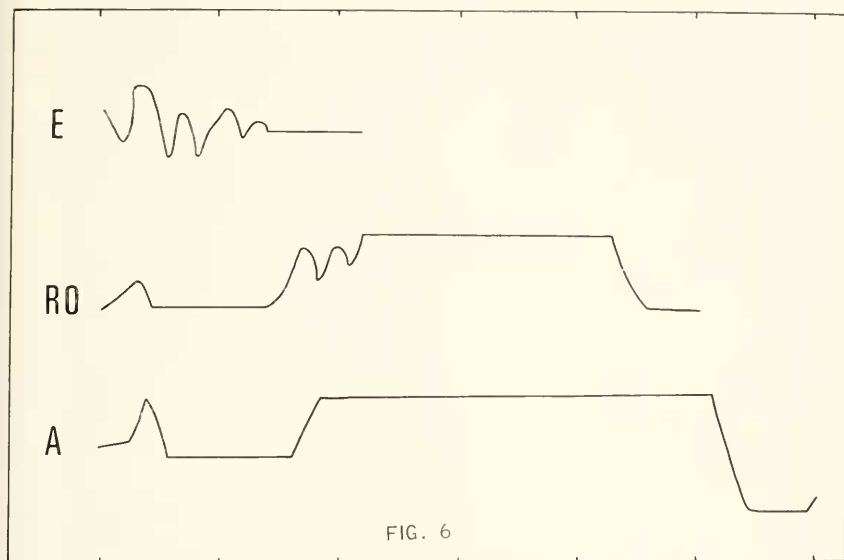
3) The pause lengths between bobbing series were also measured and the distribution of these time intervals is shown in Figure 7. Note that the first category is also the largest. This is probably an artifact — *i.e.* a pause was defined as 6 or more frames. This does not mean that it is necessarily a "real" pause to the animal. If 10 or more frames were chosen as the arbitrary limit, there would be a gradual rise in frequency to the 30-33 frame class, and then a drop. No relationship could be demonstrated between the number of peaks in a sequence and the length of the following pause.

Two other categories also easily lent themselves to quantitative analysis: number of bobbing series in a single display sequence, and total time elapsed in the full bobbing sequence. Because of the repetitious nature of the long displays and the high cost of motion picture film, few full sequences were filmed. Some examples are tabulated below:

No. bobbing series	Total time	Full sequence filmed
5	10.5 sec.	no
3	8.5	yes
5	19.3	yes
5	12.5	yes
4	12.5	no
3	6.7	yes

The total elapsed time for a full bobbing sequence in *A. luciae* is far greater than for any other member of the species group.





Figures 4-6. Head bobbing sequences in *roquet* group *Anolis*. Time intervals are one-half second between successive dots on upper and lower borders of each figure. Long pauses are indicated by a break, with the time interval in seconds written in.

Figure 4

- L. *A. luciae*
- B. *A. bonairensis*
- T. *A. trinitatis*

Figure 5

- L. *A. luciae*
- G. *A. richardi grisens*
- RI. *A. r. richardi*

Figure 6

- E. *A. roquet extremus*
- RO. *A. r. roquet*
- A. *A. aeneus*

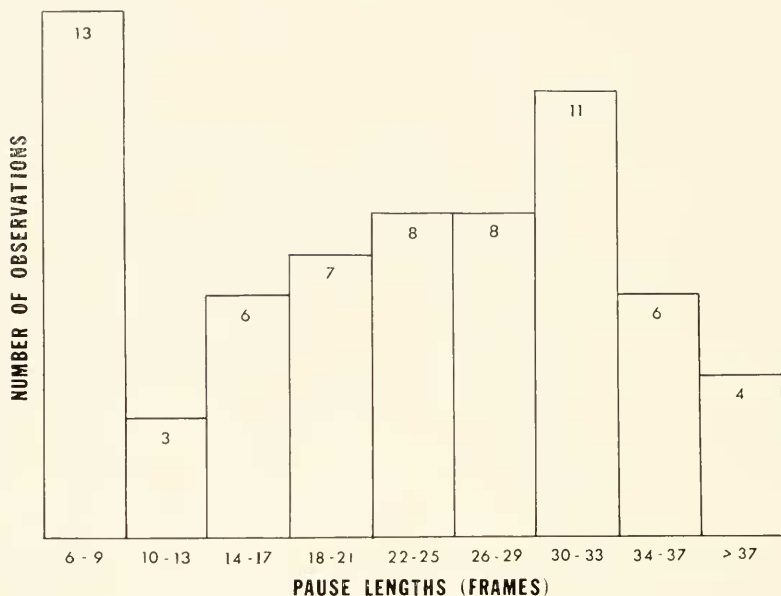


Figure 7. The frequency distribution of pause lengths which precede subsequent bobbing series in *A. luciae*. One frame is equivalent to one-sixteenth of a second.

III. PRESUMED DERIVATIVES OF *A. luciae*

A. luciae, for reasons stated earlier, is presumed to be the primitive member of the species group. Following the model presented in the zoogeographic study of the *roquet* group, three forms are believed to be derived directly from *luciae*: double colonization of St. Vincent from St. Lucia gave rise to *trinitatis* and *griseus*, and colonization of Bonaire gave rise to *bonairensis*. In this section we shall compare the displays of these three forms to those of *A. luciae*.
a) *A. bonairensis*.

The relationships of this species to the remainder of the species group are probably the least clear. Bonaire is far west of the Lesser Antillean chain (see Figure 1), but the anoles on the adjacent islands just west of Bonaire are certainly unrelated to *bonairensis*. When the species was described (Ruthven, 1923), it was compared with *roquet* and *aeneus*. The osteological study of Etheridge placed this form very close to the other members of the

roquet group, and this was confirmed by blood proteins and chromosomes. In our paper on blood proteins (Gorman and Des-sauer, 1966), it was pointed out that although *bonairensis* was clearly a member of the *roquet* group, it was not particularly close to any one form. We speculated that it might be derived from *aeneus*, since Bonaire is due west of Grenada and the general current flow is westerly.

However, when we examined chromosomes (Gorman and Atkins, 1967), we found that *bonairensis* belonged to the more primitive group ($2n=36$), making it highly improbable that it was derived from *aeneus*. The geographically intermediate form *A. bonairensis blanquillanus* has been unavailable for study.

It is, of course, possible that Bonaire was colonized independently by a mainland South American *Anolis*. However, that is not likely. Although the *roquet* group forms are clearly allied to South American alpha anoles, they share a unique complex of osteological and biochemical characters which most likely evolved in the Lesser Antilles.

Thus our hypothetical ancestor would be a *luciae*-like or *trinitatis*-like anole. J. D. Lazell, Jr., who is studying the external morphology of Lesser Antillean anoles, relates *bonairensis* to *luciae* (personal communication).

The display of *bonairensis* is basically similar to other members of the species group. It may include tail lashes and head bobs.

Description of an interaction

4 May 1964

Intruder placed on a tree. Resident male comes running across a fallen stump to stop 2 feet from intruder. He runs at least 15 feet. Head is in engorged posture. I jiggled intruder, R immediately extends dewlap fully, rises high on all four limbs, tail is raised once, dropped, body lowered. Bobs head and retracts dewlap.

The head bob sequence of *bonairensis* is unique in the large number of peaks and the great length of time. The bobbing may or may not be broken up by pauses of 6 frames or longer. In 20 filmed sequences, 14 are without pauses. These sequences have a range of 12-23 peaks (mean 17.7) and a time range of 43-95 frames (mean 62.2). Of six sequences with pauses, five have only a single pause and one sequence has two pauses. This last case may be an artifact, for the first pause follows a single slow head rise, which is probably not part of the bobbing sequence. As opposed to *luciae*, which has pause lengths of as long as 40+ frames, the

pauses of *bonairensis* are all short, ranging from 6-10 (mean 8.3) frames.

Those sequences which have pauses range in total peak number from 13-24 (mean 17.7), which is almost identical to the non-pause displays. The total time intervals range from 47-91 frames (mean 69.0), which is within the range of non-pause displays.

Thus the head bobbing sequence of *A. bonairensis* is best described as a long single sequence with many peaks, occasionally broken into two series. The display of *bonairensis* could be derived from the *luciae* display with but one minor alteration: elimination of the pauses which break the bobbing sequence into distinct series.

Bonairensis also uses tail lashing in high intensity displays. In this respect the species resembles other members of the *roquet* group more than *luciae*.

b) *A. trinitatis*.

A. trinitatis is the widespread small anole on St. Vincent. It also occurs on Trinidad, where it was probably introduced by man. On Trinidad it hybridizes with *aeneus*. A detailed analysis of hybridization is being prepared. The data on *trinitatis* presented in this paper include St. Vincent and Trinidad specimens, as no discernible difference could be found in their displays.

The challenge display of *trinitatis* consists of very rapid tail lashes followed by rapid bobs. Long pauses are infrequent. A slow tail movement has not been observed. Figure 8 compares the characteristic rapid tail movement of *trinitatis* with that of *extremus*, which is slow. Descriptions of encounters appeared in the introductory part of this paper.

The variation in 30 rapid bob sequences of *trinitatis* is:

Rapid bob time interval	No. peaks per bobbing sequence	
range (sixteenths of a sec.)	12-31	2-10
mean	23.0	5.7
	56% are 4, 5, or 6	

A typical rapid head bob of *trinitatis* is presented in Figure 4T.

The full bobbing sequence in *trinitatis* resembles a single series of bobs within a sequence in *A. luciae*. The display of *trinitatis* differs from that of *luciae* in the rapid tail lash and in the shorter, non-paused head-bob sequence. The latter, however, could easily be derived from a foreshortening of the *luciae* display.

c) *A. richardi griseus*.

Although this is the largest, it is paradoxically the shyest member of the *roquet* species group; that is, *A. r. griseus* is quick to

flee at one's approach. As a result, I have few data. No natural aggressive interactions were seen. Two males did display to tethered intruders, and their several bobbing sequences were recorded on film. These two males were filmed in the summers of 1964 and 1966, respectively, and on opposite ends of St. Vincent. The display action patterns are quite similar. Thus, although lacking details on the total range of variation display, the data are probably valid from the broadly comparative viewpoint.

High intensity display consists of dewlap extension, rapid tail lashes, head bobs, and dewlap retraction.

The head bobs are in series, as in *A. luciae*. Figure 5G illustrates a typical bobbing sequence of *griseus*.

I do not have enough pauses measured to compare in detail, but here too the distribution seems similar to *luciae*. Of 11 measured pauses, 5 are between 6-9 frames, 5 are 20 or more frames, and only one falls between these two intervals (compare with Figure 7).

There does seem to be a reduced number of peaks per series; in 18 measured series the mean is 3.3, and 61 per cent of the sequences have 1, 2, or 3 peaks. In *luciae* the mean is 5.2, and 54 per cent of the series have 4, 5, or 6 peaks. However, the mean time interval per bobbing series (16.6 frames) is very close to that of *luciae* (18.0). This implies that the head bobs of *griseus* are broader (slower) than those of *luciae*. Such a trend can be seen by comparing Figures 5L and 5G.

The total time of a bobbing sequence, adding all series and pauses, may also be shorter than in *luciae*. (Compare these data with those on p. 15.)

No. bobbing series	Total time	Full sequence filmed
2	5.0 sec.	yes
2	4.8	yes
5	8.4	yes
4	7.3	yes

In summary, the displays of *griseus* are quite similar to those of *luciae*. In head bobbing there seems to be a tendency for fewer peaks per series without a significant decrease in the time of the series, whereas the total time of a bobbing sequence is reduced.

Also, *griseus* may use several vigorous tail lashes in the challenge display, whereas *luciae* does not use the tail frequently, and does not use multiple lashes when it does use the tail.

IV. PRESUMED DERIVATIVES OF *griseus* AND *trinitatis*a) *A. r. richardi*.

A. r. richardi is very closely related to *griseus*. On the basis of blood proteins (Gorman and Dessauer, 1966), the two forms were considered conspecific and distinct from all other members of the species group.

Unlike *griseus*, *richardi* is not shy, and numerous displays have been observed in Grenada and in Bequia, the northernmost of the Grenadines. No displays were studied in Tobago.

Descriptions of encounters

1. St. George's, Grenada - 17 July 1965

A male resident is seven feet up in a mango tree. Intruder placed two feet below. R immediately into engorged head posture watching intruder. Intruder runs up. R extends dewlap fully, rises up high on all limbs, tail up a bit, then down slowly. Again up and then down slowly, dewlap still out. Intruder removed.

This is interpreted as a low intensity response. Male *richardi* may rise up slowly and the head is sometimes slowly nodded. The following is an example of a high intensity response, the type of response that was analyzed.

2. Beausejour, Grenada - 17 July 1965

Intruder placed near resident male. Dewlap extended. No tail motion. Bobs vigorously about 7 times. Dewlap partially retracted. Intruder jiggled. R rises up, lashes tail four times, then a fifth time with lower amplitude. Dewlap is held out. R looking at intruder. Intruder removed.

The high intensity display of *richardi* is characterized by vigorous tail lashing, followed by head bobbing.

Unlike *griseus*, there are not multiple series, but rather a single series, in a bobbing sequence. Figure 5 RI shows an example of *richardi* head bobs. These bobs are broad, *i.e.* the rise and fall are relatively slow and the peak is flatter than in *griseus*. The display appears much more stereotyped than that of either *luciae* or *griseus*, both in number of peaks (range 4-7, mean 5.8) and in total elapsed time in the bobbing sequence (range 39-58, mean 47.3 frames). Although there are only eight filmed displays, numerous other displays observed in the field seemed to conform to these ranges.

b) *A. aeneus*, *extremus* and *roquet*.

These three forms are very closely related and were considered conspecific by Underwood (1959), although he later changed his mind (1962). They were first studied biochemically by Gorman

and Dessauer (1965), who found that on the basis of electrophoresis of serum proteins they were closely related, and a linear chain of relationship could be established: *aeneus* and *extremus* differ in hemoglobin mobility, *extremus* and *roquet* in transferrin mobility, and *aeneus* and *roquet* differ in both these characters. In a more detailed study of blood proteins encompassing the entire species group (Gorman and Dessauer, 1966), *extremus* was recognized as a subspecies of *roquet*, and *aeneus* was recognized as a

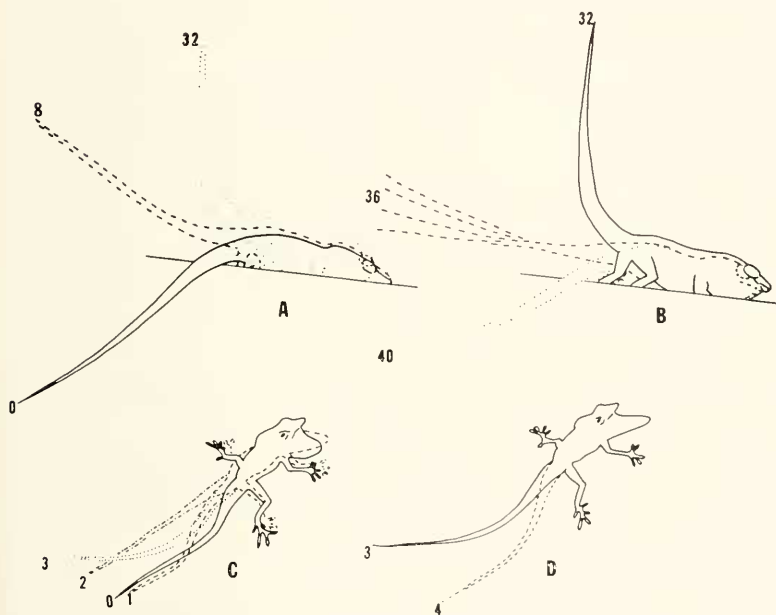


Figure 8. Comparison of the slow tail movement of *A. roquet extremus* (upper) with the rapid tail movement of *A. trinitatis* (lower). Numbers at the tip of the tail indicate frames elapsed from start of display (one frame equal to 1/16 second).

A. Tail rise in *extremus*. The tail is slowly arched up. A full two seconds elapse before peak is reached.

B. Tail lowering (same display). The tail is dropped more quickly than raised. Multiple dashes at 36 indicate tail was in rapid motion and film was blurred on that frame. Total time interval for sequence is 40 frames (2½ seconds).

C. Tail rise in *trinitatis*. The peak is reached in 3 frames.

D. Tail lowering (same display). The tail is down one frame later. Total time interval, 4 frames (¼ second). The drawings were made by superimposing images from a single frame projector.

species. The three forms are obviously very close to *trinitatis*. The chromosome study showed that *trinitatis* was a likely ancestral form, as it had the primitive chromosome number.

In display behavior, there are great similarities among the three in gross movements. That is, the sequences of movements are identical, all have a variable tail movement, slow to moderately fast — but always slower than *trinitatis* (Figure 8) — and all bob the head. But here there are consistent differences.

A. r. extremus has a head bobbing pattern that appears to be the most rigidly stereotyped. There are several rapid peaks and the display is over. There are never any long pauses. Figure 6E illustrates an example of this head bob. Thirty-two head bobbing sequences were filmed, the number of peaks per sequence ranged from 2-5 (mean 4), and the time interval in frames ranged from 6-14 (mean 10.6).

Although in blood proteins *extremus* seemed to be intermediate in this series of three forms, in head bobbing, *roquet* and *aeneus* are more similar to each other than to *extremus*. Both forms have displays characterized by a long pause; thus the total time interval of the bobbing sequence is longer than that of *extremus*. *A. r. roquet* tends to have more peaks than does *aeneus*, while *aeneus* tends to have longer pauses and thus a longer bobbing sequence. However, there is considerable overlap, as tabulated:

Rapid bob	No. peaks			Total time of bob sequence (sixteenths of a sec.)	
	no.	range	mean	range	mean
<i>aeneus</i>	(25)	2-4	2.8	27-62	44.6
<i>roquet</i>	(28)	2-9	4.3	18-47	33.3

Figures 6A and RO compare rapid bobs in the two forms.

The examples depicted accurately show the typical differences in the head bobbing sequences between the two forms. Not only are there fewer peaks and a longer pause in *aeneus*, but it also may be seen that in the typical display of *aeneus* a head rise follows the drop after the long pause, whereas in *roquet*, following the long pause the head is dropped and the bobbing sequence is terminated.

A. trinitatis is the presumed ancestor of this group. Chromosome loss being rare, it is highly probable that *trinitatis* gave rise to only one of these forms. Two alternatives are plausible.

1. Colonization of Barbados, loss of chromosome pair, giving rise to *extremus*. *A. r. extremus* then sends out two radiations, one to Martinique where a transferrin difference evolves (*roquet*), the

other to Grenada where a new hemoglobin evolves (*aeneus*). The display of *extremus* is not very different from that of *trinitatis*. Both have head-bob sequences consisting of several peaks in a short time interval. The sequence of *trinitatis* is more variable, in both number of peaks and time interval and is occasionally punctuated by pauses. The similarity in display of *roquet* and *aeneus* would have to be accounted for by convergence.

2. Colonization of Grenada, loss of a chromosome pair, giving rise to *aeneus*. Evolution of the *aeneus* type display (increase in tendency for long pause, decrease in number of peaks) is followed by colonization of Barbados (*extremus*), and from there colonization of Martinique (*roquet*). There would be minor change in the head-bob display of *roquet*, and evolution of a new head-bob display in *extremus*.

There is one other bit of behavioral evidence that can be examined to assess these two alternatives. Members of the *roquet* group have a movement which I termed "rhythmic motion." This may consist of bobbing, or walking, or climbing in a very jerky manner. The animal will move, pause, move, pause, etc. The pause is long and the movement is very sudden and exaggerated. The actual context of the display is not fully understood by me, but it appears to occur at a somewhat lower intensity than the tail movements and the rapid head bob in male-male territorial encounters.

This movement was seen most frequently in *extremus* and *aeneus*, but was also filmed occasionally in *trinitatis* and *roquet*.

In *A. r. extremus*, in eleven different displays, 100 intervals-between-bobs were measured. The range in frames (one frame = 1/16 sec.) was 5-12 (5-9 in 97 per cent of the intervals) and the mean interval between bobs is 7.27.

In *A. trinitatis* in four displays (from same individual) 30 intervals range from 7-11 with a mean of 8.46 frames.

In *A. r. roquet* only one sequence was filmed; there are 21 pauses ranging from 7-9 frames with a mean interval of 7.75.

In *A. aeneus* in ten displays 103 intervals were measured ranging from 9-19 frames with a mean of 11.9.

If this character has any meaning in terms of relationships, it implies that *aeneus* is the most divergent member of the series and that *trinitatis* is closer to *extremus*. This supports the first alternative above.

Table 1 (p. 29) summarizes some of the data for the *roquet* group.

DISCUSSION

At the level of the species group, the display behavior is useful as an additional taxonomic character. The *roquet* group can be defined as distinct from its geographic near neighbors by the absence of dewlap pumping within a display sequence. Furthermore, differences can be delineated which distinguish the eight forms of the species group.

Why stereotyped displays in island races of lizards? Why inter-island differences? Do they relate to isolating mechanisms? Among some well-established cases of vocalization in birds, island races may have much more variable, less stereotyped, and less complex calls than the corresponding mainland races (Marler, 1959). The assumption here is that there are fewer sympatric congeners, and that there is therefore reduced selection for specificity.

The few studies on island lizards, however, do not show a similar pattern. The display of *Anolis townsendi*, a species restricted to Cocos Island some hundreds of miles west of the Central American mainland, is quite stereotyped (Carpenter, 1965). Furthermore, Carpenter (1966) found, in a study similar to this one, that 11 of 12 Galapagos islands have iguanids of the genus *Tropidurus* with species-specific (or island-specific) display patterns. Each island has only one *Tropidurus*. These differences were attributed to genetic drift.

In the study by Ruibal (1967) on comparative anole behavior, island races were discussed, but the species studied were from Greater Antillean islands where each species might have a half dozen sympatric congeners at the same locality. Yet the displays described are no more stereotyped than the ones described here.

It could be argued that some of the sympatric *roquet* group anoles evolved behavioral differences as additional isolating mechanisms. For example, there was double colonization of St. Vincent from St. Lucia, which led to *trinitatis* and *griseus*. Perhaps some of the differences in the displays as seen today reflect selection for species-specific differences.

Why are the displays no less stereotyped where there is only one form on an island? Probably the least variable display in the *roquet* group is that of *extremus* from Barbados, an island which has and probably has always had only one *Anolis*.

I have attempted to emphasize that certain components in the display of each form characterize that form, yet there is some variation in the temporal sequence of displays. Since each island was colonized by a presumably small number of arrivals from

another island, population differences in display are not at all surprising. There is sampling error to begin with. Then, as the new population adjusts to the new island, there is reconstruction of the gene pool. Displays are almost certainly polygenic, virtually all genes have pleiotropic effects, and thus differences in challenge displays in anoles on isolated islands are the expected result.

But selection, too, could be playing a very strong role. When we look at the display of *A. chrysolepis* and compare it with the *roquet* group, we find few similarities. *A. chrysolepis* hardly moves its body, but flashes its cherry-red dewlap quickly; in the *roquet* group the tail is waved, the head is bobbed, and there are vigorous push-ups.

When we look at the ecology of these anoles, this behavior makes perfect sense. *A. chrysolepis* is a small brown forest anole living in deep shade. Body movements would not be conspicuous, the wind might be rustling leaves. But a sudden flash of red color appearing from "nowhere" is quite striking. Anoles in the *roquet* group are larger and display from more open sites. Thus head and body movements are conspicuous sign stimuli.

At a subtler level, this line of reasoning could account for display differences within the *roquet* group. The islands are by no means identical. Bonaire, for example, is sparsely vegetated. St. Lucia has more characteristic lush tropical flora. Could differences in the configuration of the habitat act to select for display differences? In all probability they could. Perhaps it is advantageous for *luciae* to repeat himself by giving multiple head-bobbing series while a single long series suffices in the more open terrain for *A. bonairensis*.

In cases of sympatry in the Lesser Antilles, display differences may be very important in sexual selection, even though these displays are "territorial," not "courtship," displays. In a study of two sympatric species of grackles, Selander and Giller (1961) found that males hold mutually exclusive territories and solicit nesting females of either species. It is the females that must select conspecific mates based upon a display difference. Possibly, in *Anolis*, females associate only with males giving the "proper" display. Hunsaker (1962) showed that female *Sceloporus* preferentially associated with mechanical models which gave the species-specific head-bob. Because of the importance of display in the social structure of the population, even on a one-anole island we must expect limited variation, *i.e.* stereotypy.

Despite differences in displays of all the forms considered, it should be emphasized that the basic display patterns are quite

similar and that this may be used as a valuable taxonomic character. Quite possibly, in the Greater Antilles where 20 or more species of *Anolis* may be found on a single island, there might be very strong selection for behavioral differences (including challenge display) as isolating mechanisms in closely related forms. This would render the patterns taxonomically useless, except to show that different species had different displays: it would mask, rather than elucidate patterns of relationship.

In general, the behavioral data support my proposed phylogeny of the *roquet* group based upon chromosomes and proteins. The presumed prototype, *A. luciae*, has a display which could well be the basis for further elaborations and foreshortenings, leading to the displays of the other forms. It is interesting that *luciae* and *griseus* have very similar displays, which differ from *richardi*. An entirely different approach, marshalling biochemical evidence, has led me to the conclusion that *richardi* had to be derived from *griseus* and not vice-versa (Gorman and Atkins, 1968).

The relationship between *luciae* and *bonairensis* is less clear. If *blanquillanus*, the presumed intermediate, had been available for study, this perhaps could have been clarified.

Relating *trinitatis* and *luciae* closely is not a novel idea. Underwood (1962) considered them conspecific, although his reasons were not particularly clear. The two forms differ considerably in blood proteins; however, the similarity in karyotype and certain similarities in display behavior tend to support the idea of close relationship.

To compare the different island forms I have presented the data in an oversimplified manner. That is, I implied that a display once established is static. Thus, I call *luciae* ancestral to various other forms and compare the displays of today's *luciae* to the presumed derived forms. Obviously, the displays of all forms living in isolation are subject to change. The minor use of the tail in *luciae* may well be a secondary loss rather than a primitive character that was later elaborated in all the other members of the species group.

Despite the oversimplification, however, comparative behavioral data when combined with other information are valuable in tracing the evolution and relationships of the *roquet* group.

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TABLE 1

Head bob patterns of *roquet* group anoles

Form	Peaks/Bobbing Sequence			Time Interval in 16ths of Sec.	
	No. filmed sequences	Range	Mean	Range	Mean
<i>luciae</i> ¹	83	1-18	5.2	2-47	18
<i>bonairensis</i> ²	14	12-23	17.7	43-95	62.2
<i>bonairensis</i> ³	6	13-24	17.7	47-91	69.0
<i>trinitatis</i>	30	2-10	5.7	12-31	23.0
<i>griseus</i> ¹	18	1-8	3.3	1-41	16.6
<i>richardi</i>	8	4-7	5-8	39-58	47.3
<i>extremus</i>	32	2-5	4.0	6-14	10.6
<i>aeneus</i>	25	2-4	2.8	27-62	44.6
<i>roquet</i>	28	2-9	4.3	18-47	33.3

¹ In *luciae* and *griseus*, a head bobbing sequence consists of several series of bobs, with pauses between the series. These data are for the individual series.

² In *bonairensis* there are occasionally paused displays, as in *luciae* and *griseus*. Here are tabulated non-paused displays.

³ This tabulates individual series of the paused displays.

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